

*OEDURA AND AFROEDURA (REPTILIA: GEKKONIDAE) REVISITED:  
SIMILARITIES OF DIGITAL DESIGN, AND CONSTRAINTS  
ON THE DEVELOPMENT OF MULTISCANSORIAL SUBDIGITAL PADS?*

ANTHONY P. RUSSELL AND AARON M. BAUER

Russell, A.P. and Bauer, A.M. 1990 09 20: *Oedura* and *Afroedura* (Reptilia: Gekkonidae) revisited: similarities of digital design, and constraints on the development of multiscansorial subdigital pads? *Memoirs of the Queensland Museum* 29(2): 473-486. Brisbane. ISSN 0079-8835.

The gekkonid genera *Oedura* (Diplodactylinae) and *Afroedura* (Gekkoninae) possess digits that are very similar in external morphology. These are characterised by the possession of a large, terminal pair of leaf-like scansors and a series of scansor-like plates that gradually grade into the scales of the digital bases. Such genera appear to have developed an elaborate subdigital adhesive system by encroachment of the scansorial system proximally. The genera *Diplodactylus* and *Phyllodactylus* provide potential morphotypic precursors of the digital form seen in *Oedura* and *Afroedura* respectively.

Proximal encroachment of the adhesive system involves changes in external morphology, the internal muscular and tendon systems and the integument. In both *Afroedura* and *Oedura* the perceived elaboration of the adhesive system from an external perspective is not tracked exactly by internal changes. Not all of the plates that become enlarged and hypertrophied are converted into true scansors — structures that possess some form of internal hydraulic support system in association with musculotendinous control systems and a seta-bearing integument. Only those plates that occur beneath the arcuate penultimate phalanx become elaborated into true scansors.

The genera *Oedura* and *Afroedura* may both represent independent trends towards the elaboration of multiscansorial pads. They can be employed to represent a stage in a morphotypic series towards this end, but lack the features found in multiscansorial systems, such as subdivision of both the scansors and associated sinus system beneath the penultimate phalanx, overlap of scansors, and the development of a free margin on the scansors. The development of such features may operate as constraints on the evolutionary elaboration of multiscansorial pads. □ *Gekkonidae, Oedura, Afroedura, digits, scansors, functional morphology, evolutionary constraint.*

Anthony P. Russell, Department of Biological Sciences, The University of Calgary, 2500 University Drive N.W., Calgary, Alberta, Canada T2N 1N4; Aaron M. Bauer, Biology Department, Villanova University, Villanova, Pennsylvania 19085, U.S.A.; 16 August, 1988.

The similarity of digital form in the diplodactyline genus *Oedura* and the gekkonine genus *Afroedura* was at one time thought to be of sufficient significance to unite these taxa in a single genus (Boulenger, 1888), notwithstanding their great geographic separation. Not until much later (Loveridge, 1944) was this congeneric status seriously questioned, and here certain external digital features were employed to advocate separation. Further credence was given to the separation of these two taxa as the systematics of gekkonid lizards became better known (Underwood, 1954) and different sets of characters became employed. This led to a further evaluation of their status (Cogger, 1964) and

the examination of a wide array of anatomical systems. Thus, Cogger (1964) ably demonstrated that similarities between *Oedura* and *Afroedura* were due to convergence and brought into focus questions about why such overt similarities should be so. Despite the subsequent unequivocal systematic separation of gekkonine and diplodactyline geckos (Kluge, 1967a, b), however, the basis for such similarity has remained largely unstudied. A brief attempt at addressing this question was made by Russell (1979), but the consequences of particular digital design in these two genera were only partially pursued, and the potential constraints on further elaboration of this particular design remained

largely unaddressed.

It was proposed by Russell (1979) that the digital pattern seen in *Oedura* has been developed from a condition similar to that seen in the ostensibly closely related genus *Diplodactylus* and its satellite genera *Crenadactylus* and *Rhynchoedura*. (see King, 1987, however, for an alternative but less traditional view that *Oedura* is a carphodactyline). The basis of this proposed evolutionary trend was that the simple, single pair of terminal, leaf-like scansors of *Diplodactylus* and its satellite genera had become modified into a more elaborate system by proximal recruitment of additional adhesive plates. Some species of *Diplodactylus*, such as *D. strophurus* and *D. ciliaris* possess what appear to be more proximally located incipient scansors on digits two to five, and it was proposed (Russell, 1979) that such structures were the morphological precursors of the more proximal enlarged plates in *Oedura*. Only the latter genus within the Diplodactylini possesses an adhesive system incorporating more than a single pair of scansors per digit.

Within the Gekkoninae the genus *Afroedura* possesses digits that are externally similar in form to those of *Oedura*. Given what is known about the phylogeny of the Diplodactylinae (Bauer, 1986) and Gekkoninae (Kluge, 1967b, 1983) the digital patterns of these two genera appear to have been independently evolved, with that of *Afroedura* being derived from a *Phyllodactylus*-like ancestor (Russell, 1972; Russell and Bauer, 1989). The similarity is not merely superficial, however, but also involves certain aspects of the internal control mechanisms of the seta-bearing plates (Russell, 1979). Such similarity is worthy of further scrutiny, as the independent development of very similar systems by distantly related taxa is indicative not only of similar selective pressures but also of the constraints that potentially govern the final form that systems will take. In this context we may initially assume that the behavioural component of the organism - environment interaction (Bock and von Wahlert, 1965) has played a major role in influencing the morphological parameters of the system, the major dictates being the way in which subdigital setae can be employed as effective agents of adhesion (Russell, 1975).

Morphological systems consist of integrated sets of components that must operate together if the entire system is to function (Alexander, 1975; Zweers, 1979). In the case of subdigital adhesive systems, a variety of functional and

control criteria appear to be directly correlated with the evolution of such systems in gekkonids (Russell 1975, 1976, 1981, 1986). The genera *Oedura* and *Afroedura* provide an instructive example of how canalisation (sensu Brundin, 1968) of the evolution of morphological features is involved in the elaboration of a system. Given a particular basic morphology and a particular 'problem' to be 'solved', there is only a limited amount of scope available within a given phylogenetic lineage.

The recognition of such a great degree of digital similarity between *Oedura* and *Afroedura* gives cause to pose questions about the functional reasons for such convergence. It also prompts investigation about the evolution of the system in each lineage and the potential that the increased complexity of the system has. Thus, we have here employed these two genera in order to analyse the basic features of the mechanical components (Gans, 1969) employed by each and to attempt to make some predictions about the integration of components in the evolution of digital adhesive mechanisms in gekkonids.

Taking the digits of *Oedura* and *Afroedura* as examples, we initially postulate that the adhesive systems evolved from conditions similar to those in the supposed outgroups, *Diplodactylus* and *Phyllodactylus* respectively. Here a single pair of leaf-like scansors, a means of hyperextension of the digits and the possession of a device for conforming the existing scansors to the substratum is present. Assuming that more proximal scansors are evolutionarily governed by the same functional concerns, the following predictions can be made about their elaboration from ancestrally simpler structures (subdigital scales).

(i) More scales will be added to the system in a sequential manner, from distal to proximal, and these will become modified into scansors. Thus, the distalmost of the newly acquired plates will be the most elaborate and will grade into more proximal plates that are barely distinguishable from scales, and finally into scales themselves. True scansors will be recognisable by a combination of discrete characteristics.

(ii) The elaboration of additional scansors will be associated with the elaboration of a muscular control system. Means of application of the scansors to the substratum and removal of the scansors therefrom will be associated with specific musculotendinous networks. There may not, however, be a direct and exact correlation of the recruitment of true scansors, the elaboration of setal fields, and the differentiation of the mus-

cular control systems and their tendinous networks. Thus, true scensors and subdigital lamellae should be distinguishable from each other on anatomical and histological grounds.

### MATERIALS AND METHODS

Gross morphological, internal anatomical and histological features of digits of the genera *Oedura* and *Afroedura* were examined and compared with each other and with similar features of *Diplodactylus* and *Phyllodactylus*. Dissection material and that for histological investigation was obtained from collections housed at the Australian Museum, British Museum (Natural History), California Academy of Sciences and the Transvaal Museum. The chief histological procedures employed were haematoxylin and eosin, Milligan's trichrome and Mallory's azan, protocols for which may be found in Humason (1979). Dissection and external examination was carried out on *Oedura castelnaui*, *O. coggeri*, *O. lesueurii*, *O. marmorata*, *O. ocellata*, *O. robusta*, *O. tryoni*, *Afroedura karrooica*, *A. hawaquensis*, *A. nivaria*, *A. pondolia*, *A. tembulica* and *A. transvaalica*, as well as on a variety of species of *Diplodactylus* and *Phyllodactylus*. Histological examination was conducted on *Oedura marmorata*, *O. monilis*, *O. tryoni*, *Afroedura africana*, *Diplodactylus strophurus* and *Ebenavia inunguis* (a satellite genus of *Phyllodactylus*).

### RESULTS

#### GROSS EXTERNAL MORPHOLOGY

The digits of both *Phyllodactylus porphyreus* (Fig. 1) and *Diplodactylus strophurus* (Fig. 2) are similar in external form in that they are free, relatively flat throughout their length and bear a pair of expanded, leaf-like plates at the distal end. These plates are disposed symmetrically about the claw and their bases are coincident with the articulation between the ungual and penultimate phalanx. The scales on the ventral surface of the digit are broadly expanded and extend back far proximally on the digit, but show no tendency to division or to becoming setose in any macroscopically visible sense.

In both *Afroedura* (Fig. 3) and *Oedura* (Fig. 4) the digits are also essentially flat and they each bear a pair of enlarged terminal, leaf-like plates similar to those of *Phyllodactylus* and *Diplodactylus* (Figs. 1, 2). More proximally, however, further series of enlarged plates are present that are

both divided and setose (Figs. 3, 4, 5, 6). These plates are borne proximal to the distalmost digital joint and are, therefore placed beneath the penultimate and preceding phalanges. Their number varies from digit to digit in *Oedura* (Fig. 4), with the longer digits having the greater number of elaborated plates. In *Oedura marmorata*, for example, there are three pairs of more proximal divided plates on digit two of the pes, four pairs on digits three and four, and three pairs on digit five. Digit one bears no additional divided plates (Fig. 4). Proximal to the divided plates a short series of gradually diminishing undivided plates merges with the plantar scales. The extent of the setose, more proximal divided plates is less marked in *Afroedura* in general (Fig. 3), with an additional one or two plates located on digits two to five (Onderstall, 1984). The basic arrangement is very similar to that found in *Oedura*, however, including a lack of elaboration of further divided plates on the first digit. As in *Oedura*, the more proximal scales of the digits gradually diminish in size (Fig. 3) and merge with the plantar scales (Onderstall, 1984: Fig. 6).

In both *Afroedura* (Fig. 3) and *Oedura* (Fig. 4) there is a tendency for the second pair (counting from distal to proximal) of additional divided plates to be more broadly expanded and to exhibit greater lateromesial separation than the others. This is consistent in all digits and represents a position at the base of the penultimate phalanx (see below).

#### INTERNAL GROSS ANATOMY OF THE DIGITS

In both *Phyllodactylus* (Fig. 7) and *Diplodactylus* (Fig. 8), the internal morphology of the digits is relatively simple. In both, the intermediate phalanges are short, depressed and crescentic distally, this being associated with the process of hyperextension (Russell 1975, 1976). In *Phyllodactylus* (Fig. 7) the dorsal interossei muscles do not traverse any of the phalanges fleshily and do not anastomose, but instead insert mainly at the level of the metapodial-phalangeal joint capsule of each digit. The short digital extensor muscles control the claw and the scensors, but their bellies do not extend fleshily to cross any of the phalanges (Fig. 7). At the distal end of the penultimate phalanx the tendon of each short digital extensor divides into three, with one branch continuing to insert mid-dorsally on the claw and the other two diverging to insert distally on each scensorial plate. On the flexor surface the plantar aponeurosis sends

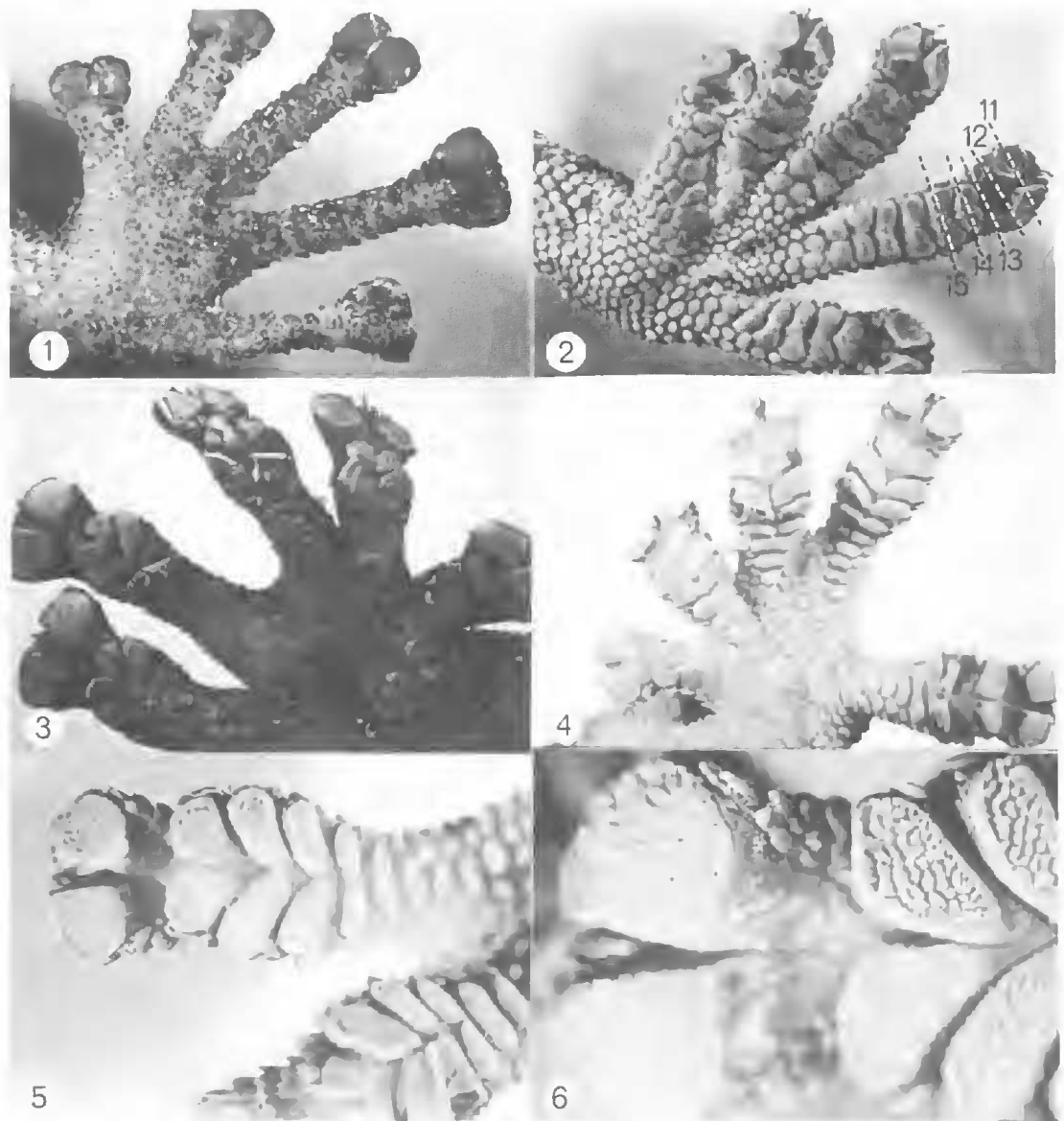


FIG. 1. Ventral view of the left pes of *Phyllodactylus porphyreus* (California Academy of Sciences - CAS 167593). Note the terminal, leaf-like scansors and the more proximal transversely expanded plates.

FIG. 2. Ventral aspect of the left pes of *Diplodactylus strophurus*. (Uncatalogued specimen). Note the leaf-like scansors and the more proximal expanded plates. The dashed lines and the numbers 11-15 represent the planes of the sections depicted in Figs. 11-15.

FIG. 3. Ventral view of the left pes of *Afroedura hawaquensis* (CAS 167638). Note the distal, leaf-like scansors and the more proximal expanded plates.

FIG. 4. Ventral view of the left pes of *Oedura marmorata* (CAS 75405). Note the terminal, leaf-like scansors and the more proximal expanded and divided plates.

FIG. 5. Ventral aspect of digit IV, left pes of *Oedura marmorata* (CAS 75405), showing the relative sizes of the distal scansor pair and the more proximal plates.

FIG. 6. Ventral aspect of digit V, left pes of *Oedura robusta* (CAS 75671), showing the setal fields on the distalmost three pairs of plates.

branches to each of the synovial metapodial-phalangeal joint capsules. Lateral digital tendons arise at these joint capsules and insert at the distal end of the antepenultimate phalanx. The lateral digital tendons thus have no contact with the scansors. The long flexor tendon extends the entire length of the digit mid-ventrally and divides distally in the manner of the short extensor tendon, to serve the claw mid-ventrally and the proximal borders of the scansors (Fig. 7). Interdigital tendinous webs are present but relatively weak, while transverse intermetatarsal and intermetacarpal ligaments are strongly developed.

The internal structure of the digits of *Diplodactylus* (Fig. 8) is architecturally very similar to that of *Phyllodactylus* described above. The short digital extensors give rise to tendons at the level of the metapodial-phalangeal joint capsules, and these traverse the phalanges (which are of the same basic form as those of *Phyllodactylus*) to insert on the claw and distal ends of the scansors. Ventrally the long flexor tendon controls the claw and the scansor pair in the same manner as that of *Phyllodactylus*, and the more proximal ventral plates are not connected with this system. The lateral digital tendons extend as far distally as the distal extremity of the antepenultimate phalanx.

In *Afroedura* (Fig. 9) the internal anatomy of the digits is somewhat more complex. The dorsal interossei muscles extend fleshily to the penultimate phalanx, and from here send a tendinous sheet to the distal extremity of the distalmost scansor pair. The more proximal pair of scansors also receives a tendinous sheet from the dorsal interossei muscles. The claw receives its extensor control from the tendon of the short digital extensor, arising from the belly of this muscle at the base of the digit.

Ventrally the branches of the plantar aponeurosis insert at the synovial metapodial-phalangeal joint capsules. These capsules are also linked by the interdigital tendinous webs and the transverse intermetacarpal and intermetatarsal ligaments. The lateral digital tendons arise from the synovial joint capsules and insert on the proximal borders of the more proximal scansor pairs. The long flexor tendon is strongly developed and serves the claw and the distalmost scansor pair, as in *Phyllodactylus*. Thus, the distalmost and more proximal scansors are controlled by different components of the flexor system. The phalanges have the same basic form as those of *Phyllodactylus*, but the penultimate phalanx

is slightly more arcuate.

Comparing the internal anatomy of the digits of *Oedura* with those of *Diplodactylus* again reveals major differences (Figs. 8,10). Here the short digital extensors have anastomosed mid-dorsally and extended fleshily as far as the proximal end of the penultimate phalanx (Russell, 1979). The architecture of the modified short digital extensors (Fig. 10) is similar to that of the dorsal interossei of *Afroedura* (Fig. 9). Here, however, the mid-dorsal tendinous raphe gives rise to individual tendons that insert distally on each of the scansor pairs, including the distalmost. A mid-dorsal tendon also continues distally to insert on the claw. The plantar aponeurosis and associated ligamentous strands are similar to those of *Afroedura*. The long flexor tendon splits distally to serve the claw and the distalmost scansor pair, as in *Diplodactylus*, while the lateral digital tendons serve the more proximal scansor pairs in a manner similar to that in *Afroedura* (Figs. 9,10). The phalanges of *Oedura* are similar to those of *Diplodactylus*, but the penultimate phalanx is more arcuate.

#### HISTOLOGICAL DETAILS

Gross dissection of the digits of all four genera in question reveals that blood sinuses are present in the digits. The extent of these and their tributaries is only evident, however, if sections of the digits are examined.

In *Phyllodactylus* (Dellit, 1934:Fig. 13) and *Diplodactylus* (Fig. 11) a sinus is present but is restricted to the distalmost part of the digit and is associated with the penultimate and unguis phalanges. The sinus is a paired structure distally, with the unguis phalanx intervening between its two halves (Fig. 11). Immediately proximal to the distal scansor pair the sinus diminishes in size (Fig. 12) and finally disappears as a discrete structure in the hinge region between the scansor bases and the next most proximal plate (Fig. 13). The next most proximal plate is undivided and bears a smaller, but none the less distinct, expanded sinus that is mostly concentrated over the central part of the plate (Fig. 14). This plate resides beneath the penultimate phalanx. The next more proximal plate is borne beneath the antepenultimate phalanx. It is single but shows some sign of incipient division centrally (Fig. 15). This plate bears setae but appears to be cushioned primarily by vacuolar adipose tissue (Fig. 15). The difference in size of the sinuses of the distalmost and next more proximal plates can be more fully appreciated in longitudinal section



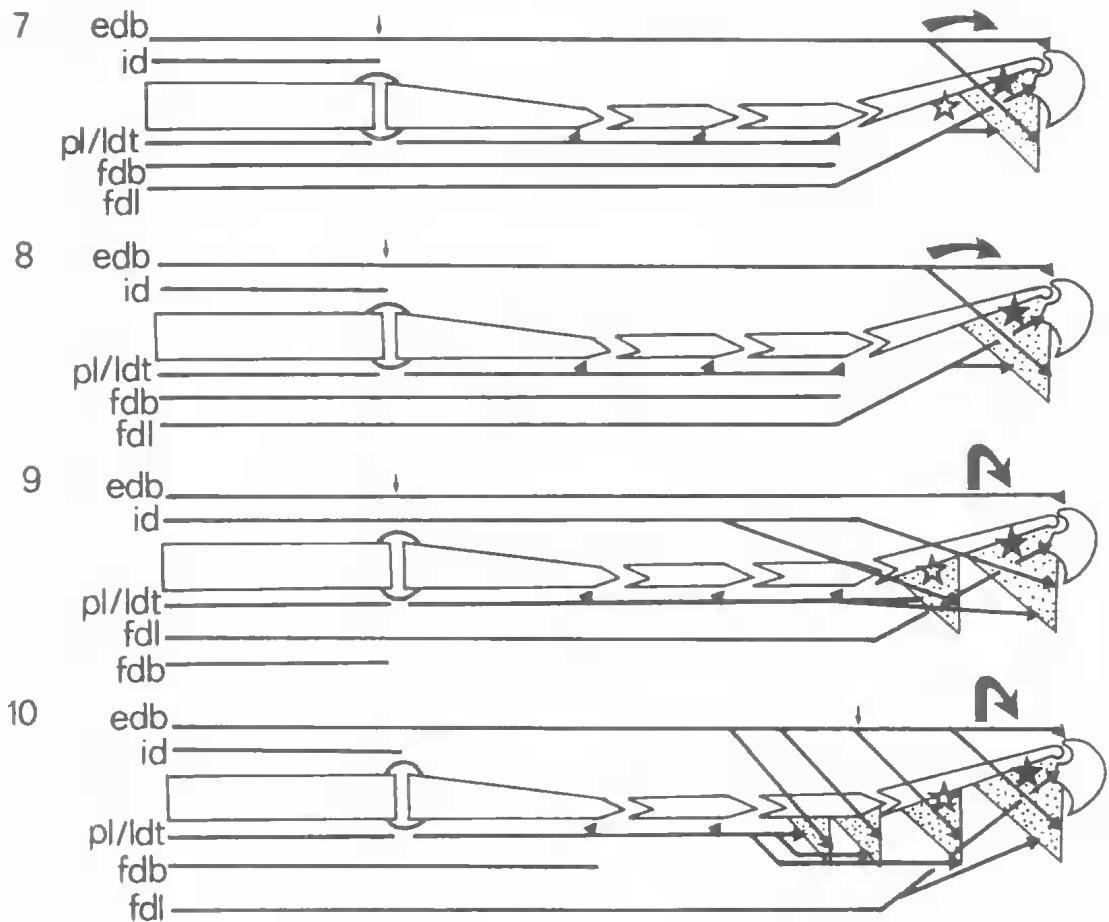


FIG. 7. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Diplodactylus*. The block-like structures represent the metatarsal and the phalanges, those with chevron-shaped ends being the phalanges involved in hyperextension. The muscles are represented by black lines, with arrow heads indicating their insertions. The large, black arrow represents the relatively mild curvature of the penultimate phalanx. Blood sinuses are represented by stars, the primary one being solid and the secondary one open. The scansors are stippled. The hoop-like structure connecting the metatarsal (the large block to the far left) with the first phalanx (the block to the immediate right of this) represents the metatarsophalangeal joint capsule. Abbreviations: edb, extensor digitorum brevis; fdb, flexor digitorum brevis; fdl, flexor digitorum longus; id, interossei dorsales; pl/ldt, plantar aponeurosis/lateral digital tendon continuum. The small, vertical arrow represents the distal extent of the fleshy belly of the extensor digitorum brevis.

FIG. 8. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Phyllodactylus*. The symbolism and abbreviations are as for those of Fig. 7.

FIG. 9. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Afroedura*. The symbolism and abbreviations are as for those of Fig. 7 except for the large, black arrow that represents a greater curvature of the penultimate phalanx.

FIG. 10. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Oedura*. The symbolism and abbreviations are as for those of Fig. 9. Note that in *Oedura* the extensor digitorum brevis controls the hyperextension of the scansors, while in *Afroedura* this is achieved by the interossei dorsales.

(Fig. 16), together with the absence of any appreciable sinus development in the most distal of the plates beneath the antepenultimate phalanx. The penultimate plate may be considered as an incipient scansor.

The stratum compactum of the dermis of the distal-most plates is strongly developed at their bases (Fig. 17). This is associated with the long flexor tendon. In the more proximal plates there is incipient development of a strong basal stratum compactum, especially in the most distal of the single plates. As one passes proximally the plates become less well-developed in this regard (Fig. 17), although they are cushioned by adipose-like tissue. The more proximal manifestations of the stratum compactum may be associated with the lateral digital tendons.

In *Oedura* and *Afroedura* the extent of the setal fields is greater than it is in *Phyllodactylus* and *Diplodactylus*, and to some extent this is reflected in the internal anatomy. In *Oedura monilis* the sinus associated with the distal-most pair of plates is massive and single, but sends branches into both sides of the terminal pad (Fig. 18). This is associated with what appears to be vertically stacked columns of smooth muscle associated with the walls of the sinuses (Fig. 18). Further proximally the sinus diminishes in size and then appears again as an appreciable expansion in the next most proximal, and divided, plate. This pair is borne beneath the penultimate phalanx. Here, however, the sinus is somewhat smaller, more diffuse and more markedly paired (Fig. 19). A large amount of fibrous connective tissue is present centrally, above the division between the two halves of the penultimate plate. As in *Diplodactylus*, only the distal-most and the next most proximal plates are housed ventral to the penultimate phalanx. The next more proximal pair of plates is present beneath the antepenultimate phalanx (Fig. 20), and here the involvement of the vascular system is minimal. In longitudinal section the diminution in extent of involvement of the vascular system in the plates is evident (Fig. 21), as is the arcuate nature of the penultimate phalanx and the basal development of the stratum compactum in the scansors proper and the more proximal plates. More laterally the association of the columns of smooth muscle cells with the sinus in the distal-most scansor pair, the extent of the sinus system in the next most proximal scansor pair and the sharp demarcation between these and the more proximal plates can be seen (Fig. 22).

#### SETAL DIFFERENTIATION.

Comparing *Diplodactylus* with *Oedura* (and *Phyllodactylus* with *Afroedura*) it can be seen that setae are associated with subdigital plates that exhibit a hypertrophied epidermis (Figs. 16,21). There is a sharp demarcation between these plates and more proximal, typical scales. Viewed with the light microscope there does not appear to be a significant diminution in size of the setae from distal to proximal, even though the internal structure of the plates that bear them differs considerably. The more distal plates are associated with the blood sinus system while the more proximal ones have little or no such association and are instead filled with vacuolar, adipose-type tissue. Those plates exhibiting the seta-bearing (Schleich and Kästle, 1986: plate 6, fig. 3), hypertrophied epidermis occur beneath the hyperextensible phalanges (phalanges two to five in digit four) (Figs. 16,21). A comparative survey of the potential differentiation of spines, spikes, prongs and setae on the various subdigital scales and plates, similar to that performed by Peterson (1983) for anoline iguanids, remains to be carried out.

#### DISCUSSION

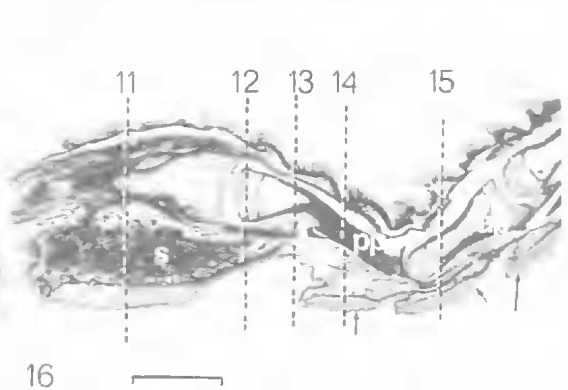
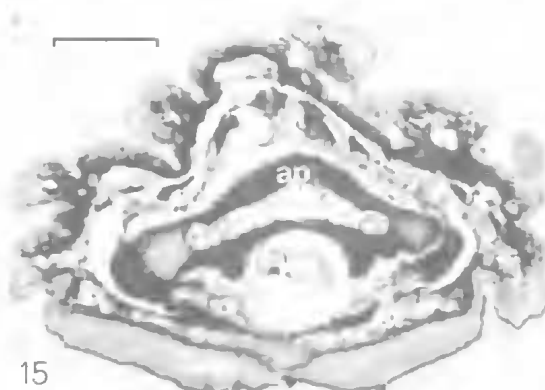
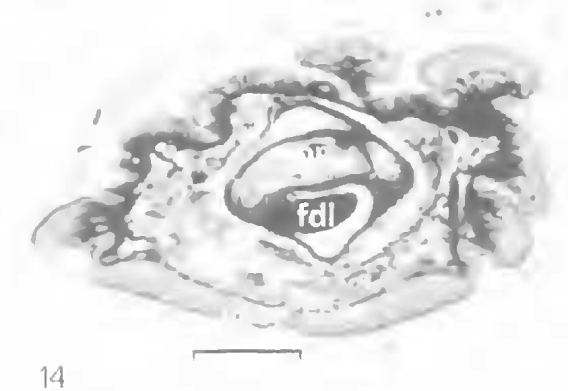
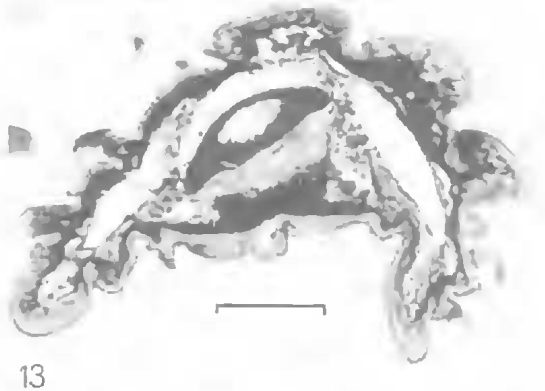
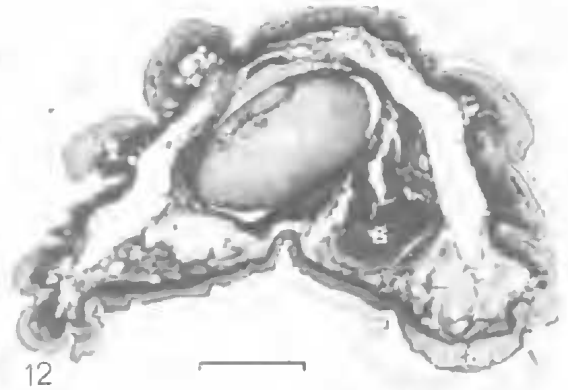
The data outlined above make it possible to make some deductions about the development of a subdigital, adhesive apparatus and about the distinction between scansors and 'lamellae'. The scenario outlined by Russell (1976) that lineages that initially develop distal scansors may expand the subdigital pads by extending the scansor series proximally is the premise upon which the deductions below are based.

Comparisons of *Phyllodactylus* and *Afroedura* from the Gekkoninae and *Diplodactylus* and *Oedura* from the Diplodactylinae provide two independent morphotypic series in which trends can be compared. In both there is a tendency to elaborate the size of the proximal plates on digits two to five, to divide them and to increase the seta-bearing surface area. This may be postulated to be a means of increasing adhesive efficiency, although empirical tests of this in standardised conditions, or rigorous comparisons of the details and physical properties of preferred locomotor substrata are not available (Bauer and Good, 1986). In both putative lineages an adhesive system is primitively present, relying on the employment of a pair of distinct and enlarged distal leaves. These are morphologically sharply demarcated from the

more proximal digital plates. The digits of both *Phyllodactylus* and *Diplodactylus* are capable of hyperextension (Russell, pers. obs.) and this activity is practised during normal locomotion. The musculotendinous systems that bring these movements about are relatively simple, but possess all of the basic requisites deemed to be necessary for such activity (Russell 1975, 1976). The distal plates are true scansors (Russell 1981), as adjudged by their possession of setae, a mechanism enabling them to be hyperextended, and an internal hydraulic device that permits these plates to conform to irregularities

of the substratum and thus make optimal contact (Russell, 1981). In this case the hydraulic device is present as a vascular sinus system, but other mechanisms also exist (Russell, 1972, 1979).

More proximally the next plate may be categorised as an incipient scansor. It bears setae, may be hyperextended, but possesses only a relatively small sinus system, making conformation with the substratum potentially less effective. This more proximal plate is borne beneath the penultimate phalanx, which arches away from the substratum and permits the housing of the central component of the sinus system





beneath it (Russell, 1981). Proximal to this the plates do not possess the properties of true scansors in as much as the sinus system, or some other hydrostatic device that can be pressurised, is not incorporated. This appears to be due largely to the morphology of the intermediate phalanges (phalanges two and three in digit four) that are associated with hyperextension. Typically these are depressed and wide (Russell, 1975) and remain firmly adpressed to the substratum (Russell, 1976). Their morphology precludes the incorporation of a centralised sinus or similar device beneath them. The presence of such phalanges in forms that develop distal scansors may later act as a constraint on the potential for further digital modification as they may preclude the development of true scansors beneath them (see below). Forms that have developed scansors from the base of the digits distally have a different constructional arrangement of the intermediate phalanges (Russell, 1977).

Further elaboration of the control systems of the digits in *Afroedura* and *Oedura*, as compared to their putative morphotypic precursors, has not brought about a concomitant increase in the number of scansors, if the criteria for their recognition, as outlined above, are applied. Here the mechanisms of application of the subdigital

plates to the substratum and their removal from it can apparently be more precisely controlled, as deduced from the increased complexity of the musculotendinous features of the digits. Examination of histological detail reveals, however, that although the sinus system remains elaborate in the distal pair of plates and has become more elaborate in the next most proximal pair, it is not evident proximal to this. Thus, although externally the yet more proximal plates have become more prominent and more scansor-like (more so in *Oedura* than *Afroedura*) in appearance, their internal differentiation is not so marked. Thus, in the proximal encroachment of subdigital pads from a distal beginning, more than external elaboration is required to convert these structures into fully-differentiated scansors. It appears that one constraining parameter is the ability to incorporate a sinus system into a pad consisting of multiple scansors. Here, the incorporation of scansors beneath the penultimate phalanx becomes critical. This phenomenon was noted for the tokay (*Gekko gecko*) by Russell (1981: Fig. 7). Here, multiple scansors are present beneath the penultimate phalanx and these possess branches of an elaborate sinus system. Proximal to this the lamellae bear setae but are morphologically

FIG. 11. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the terminal, leaf-like scansors at the base of the claw. See Figs. 2 and 16 for position of section. The sinus (s) is large and is positioned ventral to the unguis phalanx (up). At this point the sinus is paired, one half being associated with each leaf of the scansor (scan). The scale bar = 0.25mm. Mallory's azan stain.

FIG. 12. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the base of the distal scansor pair. See Figs. 2 and 16 for position of the section. At this point the sinus (s) is paired but smaller and lies beneath the distal cartilaginous epiphysis (ep) of the penultimate phalanx. The section is somewhat oblique, with the right leaf and sinus being represented more proximally than the left, where the scansor base (scan) is still visible. The scale bar = 0.25mm. Mallory's azan stain.

FIG. 13. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the hinge region between the distal scansor pair and the next most proximal plate. See Figs. 2 and 16 for position of the section. The sinus (s) is much reduced at this point and is present only as a connecting channel between the scansors and the penultimate plate. The penultimate phalanx (pp) is depressed and transversely widened at this point. The scale bar = 0.25mm. Mallory's azan stain.

FIG. 14. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the undivided penultimate plate. See Figs. 2 and 16 for position of the section. The sinus (s) is expanded again and is present beneath the penultimate phalanx (pp) and associated tendon of the flexor digitorum longus (fdl). The incipient scansor (incip. scan) bears no central thinned area. The scale bar = 0.25mm. Mallory's azan stain.

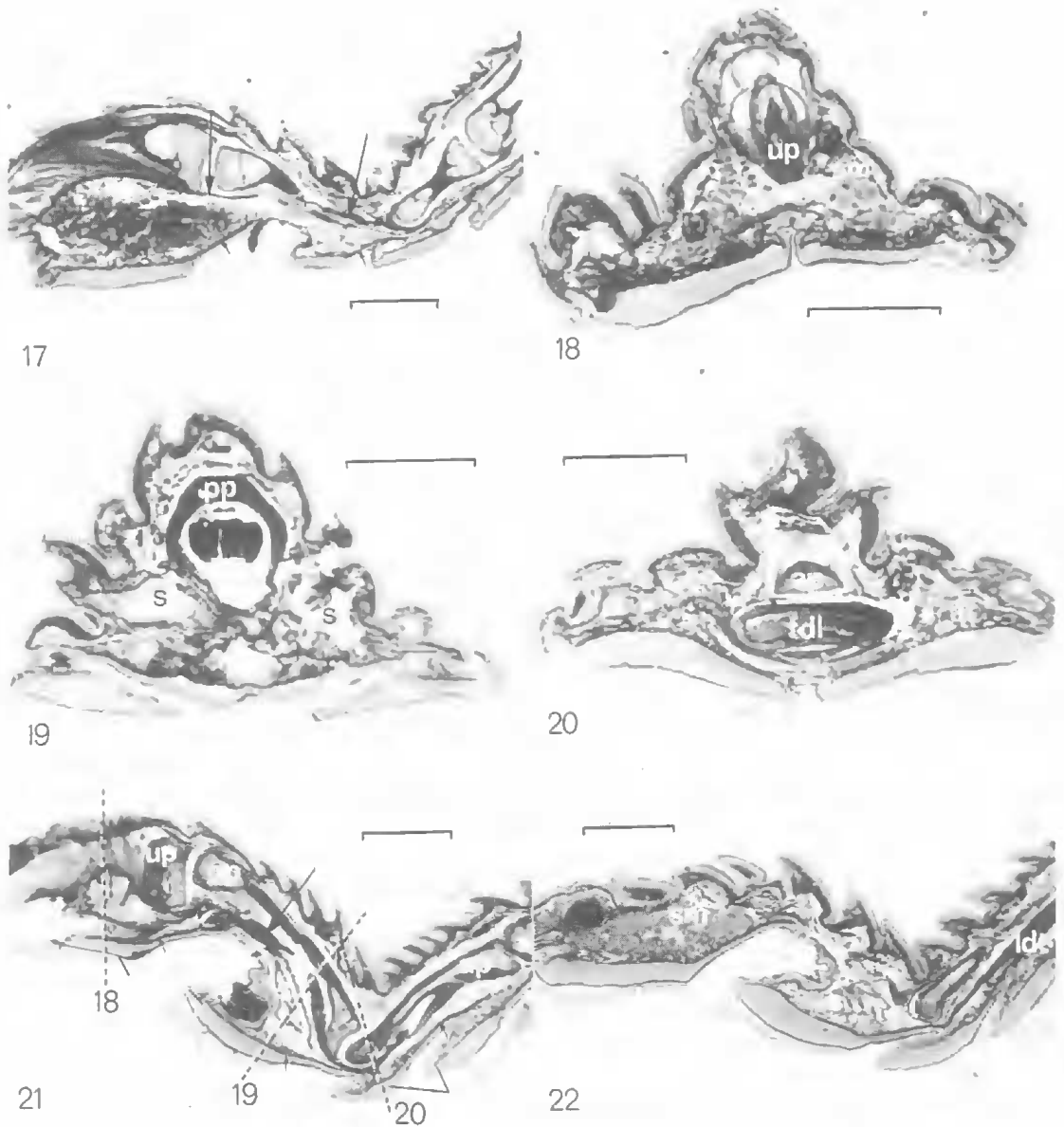
FIG. 15. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the antepenultimate plate, beneath the antepenultimate phalanx (ap). See Figs. 2 and 16 for position of the section. The sinus is not evident and the lamella (lam) is cushioned by vacuolar adipose tissue (at). The tunnel for the tendon of the flexor digitorum longus (fdl) is evident. The scale bar = 0.25mm. Mallory's azan stain.

FIG. 16. Longitudinal section of digit IV, left pes of *Diplodactylus strophurus* showing the relationships of the sinus (s), scansors (scan), incipient scansor (incip. scan), lamellae (lam), unguis (up), penultimate (pp) and antepenultimate (ap) phalanges. The dashed lines and the numbers 11-15 represent the planes of the sections depicted in Figs. 11-15. The scale bar = 0.5mm. Mallory's azan stain.

much less elaborate, bearing a closer resemblance to true scales than do the scansors. Again there is probably a functional correlate of this differentiation, as the scansors are more likely to be able to maximise contact with the substratum (on at least some locomotor surfaces) due to their additional compliance. In the tokay (and many other geckos having multiple scansors) the adhesive properties are probably further enhanced by the overlapping nature of the scansors (Fig. 23) and the sequential effect of the reticular network of the sinus system of one scansor on the setae of the next most proximal

scansor (Russell, 1981). In *Oedura* and *Afroedura* the scansors do not overlap and do not have the free border typical of those of the tokay (Fig. 23), so again the adhesive efficiency is potentially limited.

The digital conditions in *Oedura* and *Afroedura* appear to be indicative of a transitional phase (in the sense of evolutionary morphology rather than phylogeny) between a single scansor system and a multiscansorial system. These taxa do, therefore, provide us with some insight as to how the latter may have evolved from a morphologically less complex condition.



The transition as visualised in a morphotypic sequence is not smooth, however, and the differences between the *Gekko* system (typifying multiscansorial pads) and the *Oedura* and *Afroedura* systems are quite marked. The differences seen may be indicative of a syndrome of characters that are synonymous with the evolution of a multiscansorial system, and functional constraints may operate either to govern the potential transition or to prevent it. The sequence by which multiscansorial pads arose is not known, but examination of the condition of the digits in *Oedura* and *Afroedura* provides one means of attempting to understand how this may have come about. Further anatomical and histological investigations of other genera will be helpful in attempting to assess the feasibility of the proposed scheme. A similar scheme erected for anoline iguanids (Peterson, 1983) suggests a similar set of related morphological events, although her assessment was based entirely on external features.

Given what can be potentially deduced about digital form and evolution in the *Diplodactylus* - *Oedura* and *Phyllodactylus* - *Afroedura* mor-

photypic sequences, the following represents a relative chronology of changes in the adhesive system based upon the constraints as outlined. This chronology attempts to firstly account for the transition from a single pair of terminal, leaf-like scansors to the elaboration of more proximal pairs, as exemplified by *Oedura* and *Afroedura*. Secondly it attempts to explain how the latter conformation may be morphologically extended into a multiscansorial system (or alternatively how it may be limited by the magnitude of the morphological gaps that are evident).

1. The pattern begins with a pair of terminal, leaf-like scansors with extensive setal fields and a well-developed blood sinus system. The digit is able to be hyperextended. The proximal part of the digit is flat and the transversely widened plates beneath are endowed with setae as far proximally as the distal end of the first phalanx. The most distal widened plate is positioned ventral to the penultimate phalanx and possesses an incipient sinus. This is the condition exemplified by *Phyllodactylus* and *Diplodactylus*. This stage suggests that seta-bearing lamellae precede the development of true scansors both

FIG. 17. Longitudinal section of digit IV, left pes of *Diplodactylus strophurus* showing the stratum compactum of the dermis of the scansors and penultimate plate (small arrows), this being associated with the long flexor tendon (large arrows). The scale bar = 0.5mm. Mallory's azan stain.

FIG. 18. Cross section of digit IV, left pes of *Oedura monilis* through the terminal, leaf-like scansor pair. See Fig. 21 for position of the section. The large central sinus (s) is evident, together with its associated smooth muscle columns (sm). The sinus resides beneath the unguis phalanx (up) and cushions the scansors (scan). The scale bar = 0.5mm. Mallory's azan stain.

FIG. 19. Cross section of digit IV, left pes of *Oedura monilis* through the penultimate scansor pair. See Fig. 21 for position of the section. The sinus (s) is paired and smaller than that of the distalmost scansor pair. The penultimate scansor pair (scan) resides beneath the penultimate phalanx (pp). Fibrous connective tissue (fct) fills the space above the cleft between the leaves of the scansor pair. The scale bar = 0.5mm. Mallory's azan stain.

FIG. 20. Cross section of digit IV, left pes of *Oedura monilis* through the antepenultimate pair of plates. See Fig. 21 for position of the section. The lamellae (lam) are cushioned only by adipose tissue (at) and reside beneath the antepenultimate phalanx (ap) and its associated tendon of the flexor digitorum longus (fdl). The scale bar = 0.5mm. Mallory's azan stain.

FIG. 21. Longitudinal section of digit IV, left pes of *Oedura monilis* showing the relationships of the sinus (s), scansors (scan), lamellae (lam), unguis (up), penultimate (pp) and antepenultimate (ap) phalanges. The stratum compactum of the dermis of the scansors (small arrows) is evident. That of the distal scansor pair is associated with the tendon of the flexor digitorum longus (large arrow), while that of the penultimate scansor pair is associated with the lateral digital tendon (out of the plane of the section, but see Fig. 22). The dashed lines and the numbers 18-20 represent the planes of the sections depicted in Figs. 18-20. The scale bar = 0.5mm. Mallory's azan stain.

FIG. 22. Parasagittal section of digit IV, left pes of *Oedura monilis*, showing the columns of smooth muscle (sm) associated with the distal scansor pair and the extent of the sinus (s) of the penultimate scansor pair. The lateral digital tendon (ldt) and its association with the stratum compactum of the penultimate scansor pair is evident. Note the absence of a free distal margin on the scansors (compare with Fig. 23) and the sharp demarcation between the scansors and the more proximal lamellae. The scale bar = 0.5mm. Mallory's azan stain.

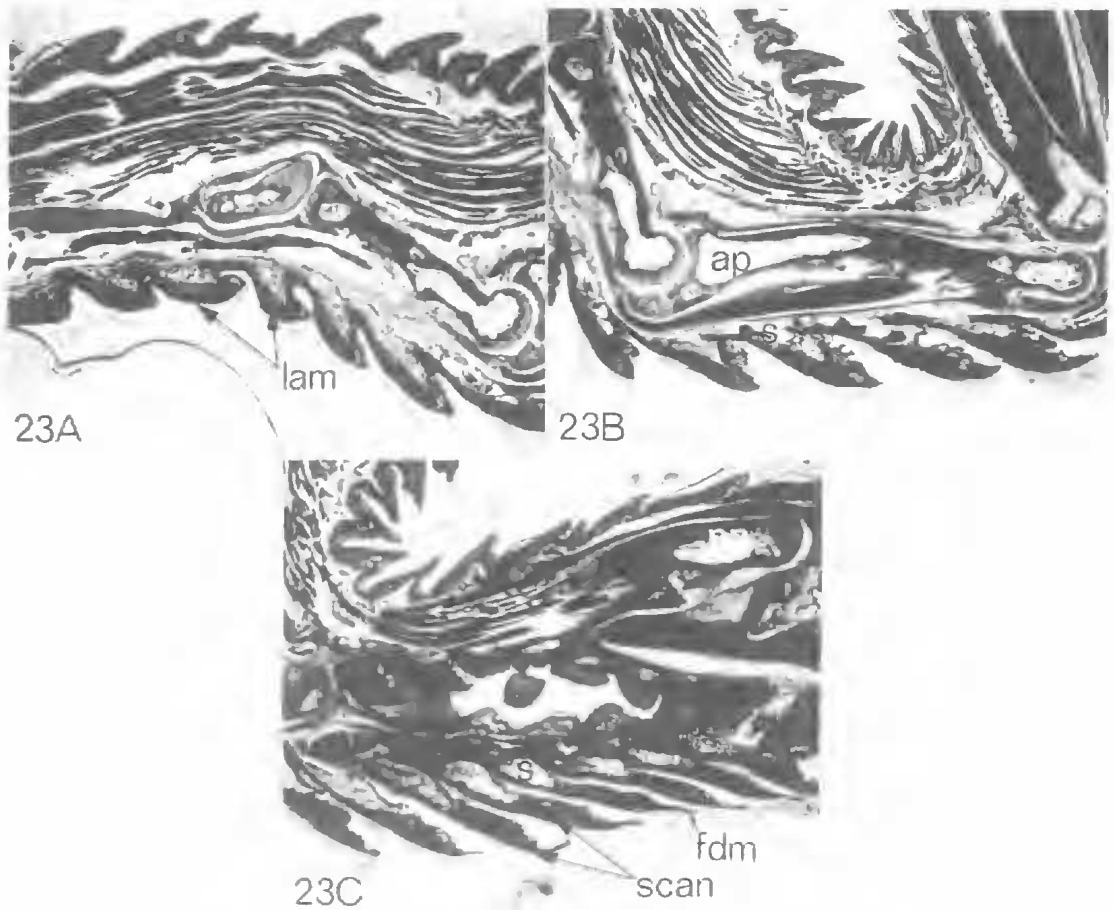


FIG. 23. Scansor and lamellar differentiation in *Gekko gecko*. A. represents a longitudinal section through the proximal region of digit IV, left pes. Here the subdigital plates bear short setae but lack a free distal margin and an involvement of the sinus system. B. represents a longitudinal section through the region of the antepenultimate phalanx. Here the free distal margin is slightly developed and the sinus system is partially involved. C. represents the region of fully differentiated scansors beneath the penultimate phalanx. Note the multiple scansors in this region, the extensive involvement of the sinus system, the extensive overlap of the scansors and the extensive free distal margin on each scansor. Abbreviations: ap, antepenultimate phalanx; fdm, free distal margin; lam, lamellae; pp, penultimate phalanx; s, sinus; scan, scansors.

evolutionarily and positionally. This suggests that adhesive systems begin by employing expanded plates with setose surfaces (lamellae). Subsequently these may be modified to become true scansors, and this may increase adhesive efficiency.

2. The adhesive system is elaborated by a proximal encroachment of scansor-like plates, enhancing the possibility of surface contact by elaborating the core of the plate by the development of vacuolar, adipose-like tissue. The distal scansors remain well-developed and the next

most proximal plate gives rise to leaves that possess a greater elaboration of the sinus system. The penultimate phalanx is more arcuate and true scansors reside beneath this. Proximal to this the scansor-like plates are enlarged and prominent but lack branches of the sinus system. The proximal plates may thus increase the adhesive power of the digits, but they do not have the flexibility for conformity with the locomotor substratum that the true scansors do, with their sinus systems. The distal scansor pair is controlled in its flexor aspect in the same way as in

*Diplodactylus* and *Phyllodactylus*, while the more proximal plates receive their flexor control from the lateral digital tendons. Only the most distal of these is a true scansor. The extensor control of the plates has been taken over by the distal migration of muscle bellies into the digit proper, and these traverse all but the penultimate and distalmost phalanges. The scansors and more proximal plates are controlled on the extensor surface in essentially the same way. This is essentially the condition in *Afroedura* and *Oedura*, although in the former the plates have not progressed as far proximally as they have in the latter.

3. The trend so far outlined appears to be one that is leading towards the elaboration of multi-scansorial pads, but both *Afroedura* and *Oedura* lack certain features that are typical of a multi-scansorial system. In order to continue the trend to give rise to such a pad the following changes would be predicted to take place (based on a comparative survey of scansor and pad design in general): The distal scansor pair would become reduced in size, giving the claw a greater degree of freedom from the pad. In association with this the scansor pair beneath the penultimate phalanx would become subdivided as the penultimate phalanx became more arcuate (This is seen also in the gekkonine genus *Calodactylodes*). The sinus system would become subdivided, with the reticular networks of the scansors being confined to their bases. As the scansors subdivided there would be a trend to the elaboration of a free, distal, seta-bearing margin that would become overlain by the reticular network of the next most distal scansor. True scansors would be restricted to the area beneath the penultimate phalanx. Proximal to this, enlarged plates would bear fields of setae but would not possess branches of the sinus system. These plates would lack the free margin and would remain essentially similar to the more proximal plates seen in *Diplodactylus* and *Oedura*. The constraints of the incorporation of components of the venous sinus system and the restriction to elaboration of scansors to the region immediately below or adjacent to the penultimate phalanx dictate to a large degree how the system as seen in *Oedura* and *Afroedura* may be further elaborated.

Cogger (1964) was intrigued with the phenetic similarity of, but apparent lack of phylogenetic affinity between, *Oedura* and *Afroedura*. He carefully documented the similarities and differences between these two taxa and correctly surmised that the similarities were due to conver-

gence. Although Cogger (1964) indicated that similarities of foot structure were superficial, they are, in fact, quite extensive. The arrangement of components and their integration indicate that the independent acquisition of this basic pattern has been governed by very similar selective factors relating to the functional control of the scansor system. Both genera appear to exhibit a morphologically intermediate condition between a relatively simple adhesive system and one that is considerably more complex. The potential limits and constraints on both genera, in terms of further elaboration of their subdigital adhesive apparatus, appear to be rather similar and represent an example of how functional demands can potentially canalise (Brundin, 1968) an evolving system.

#### ACKNOWLEDGEMENTS

We thank Darcy Rae for the preparation of the histological material used in this study. Specimens examined were made available from the collections of the Australian Museum (AMS), the British Museum (Natural History) (BMNH), California Academy of Sciences (CAS), and the Transvaal Museum (TM). We thank Allen Greer, Nick Arnold, Robert Drewes and Wulf Haacke respectively for the loan of spirit preserved and skeletal material, and for giving permission to dissect specimens and prepare material for histological examination. Merle Marsden Jr provided general assistance in the laboratory. Financial support for the completion of this work and to assist in travel to Brisbane to present this contribution at the Australian Herpetological Conference was provided in part by a Natural Sciences and Engineering Research Council of Canada grant (No. A9745) to A.P.R. and in part by a University of Calgary postdoctoral fellowship to A.M.B. The manuscript was typed by Susan Stauffer.

#### LITERATURE CITED

- ALEXANDER, R. MCN. 1975. Evolution of integrated design. *Amer. Zool.* 15: 419-425.
- BAUER, A.M. 1986. Systematics, biogeography and evolutionary morphology of the Carphodactylini (Reptilia: Gekkonidae). (Unpublished Ph.D. thesis, University of California, Berkeley).
- BAUER, A.M. AND GOOD, D.A. 1986. Scaling of scansorial surface area in the genus *Gekko*, pp. 363-366. *In* Rocek, Z. (ed.), 'Studies in



- herpetology'. (Charles University; Prague)
- BOCK, W.J. AND VON WAHLERT, G. 1965. Adaptation and the form- function complex. *Evolution* 19: 269-299.
- BOULENGER, G.A. 1888. On new and little-known South African reptiles. *Ann. Mag. Nat. Hist.* (6)2: 136-141.
- BRUNDIN, L. 1968. Application of phylogenetic principles in systematics and evolutionary theory, pp. 473-495. *In* Ørving, T. (ed.), 'Current problems of lower vertebrate phylogeny' (Interscience; New York).
- COGGER, H.G. 1964. The comparative osteology and systematic status of the gekkonid genera *Afroedura* Loveridge and *Oedura* Gray. *Proc. Linn. Soc. N.S.W.* 89: 364-372.
- DELIIT, W.-D. 1934. Zur Anatomie und Physiologie der Geckozehne. *Jena Z. Naturwiss.* 68: 613-656.
- GANS, C. 1969. Functional components versus mechanical units in descriptive morphology. *J. Morphol.* 128: 365-368.
- HUMASON, G.L. 1979. 'Animal tissue techniques'. (W.H. Freeman and Co.; San Francisco).
- KING, M. 1987. Chromosomal evolution in the Diplodactylinae (Gekkonidae: Reptilia). I. Evolutionary relationships and patterns of change. *Aust. J. Zool.* 35: 507-531.
- KLUGE, A.G. 1967a. Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Aust. J. Zool.* 15: 1007-1108.
- 1967b. Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Amer. Mus. Nat. Hist.* 135: 1-60.
1983. Cladistic relationships among gekkonid lizards. *Copeia* 1983: 465-475.
- LOVERIDGE, A. 1944. New geckos of the genera *Afroedura*, new genus, and *Pachydactylus* from Angola. *Amer. Mus. Novitates* 1254: 1-4.
- ONDERSTALL, D. 1984. Descriptions of two new subspecies of *Afroedura pondolia* (Hewitt) and a discussion of species groups within the genus (Reptilia: Gekkonidae). *Ann. Transvaal Mus.* 33: 497-509.
- PETERSON, J.A. 1983. The evolution of the subdigital pad in *Anolis*. I. Comparisons among the anoline genera. pp. 245-283. *In* Rhodin, A.G.J., and Miyata, K. (eds), 'Advances in herpetology and evolutionary biology'. (Harvard University Press; Cambridge, Massachusetts).
- RUSSELL, A.P. 1972. 'The foot of gekkonid lizards: a study in comparative and functional anatomy'. (Unpublished Ph.D. thesis, University of London).
1975. A contribution to the functional analysis of the foot of the tokay, *Gekko gecko* (Reptilia: Gekkonidae). *J. Zool. Lond.* 176: 437-476.
1976. Some comments concerning interrelationships amongst gekkonine geckos. pp. 217-244. *In* Bellairs, A. J'A. and Cox, C.B. (eds), 'Morphology and biology of reptiles'. (Academic Press; London).
1977. The phalangeal formula of *Hemidactylus* Oken, 1817 (Reptilia: Gekkonidae), a correction and a functional explanation. *Zbl. Vet. Med. C. Anat. Hist. Embryol.* 6: 332-338.
1979. Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. *Copeia* 1979: 1-21.
1981. Descriptive and functional anatomy of the digital vascular system of the tokay, *Gekko gecko*. *J. Morphol.* 169: 293-323.
1986. The morphological basis of weight-bearing in the scapulae of the tokay gecko (Reptilia: Sauria). *Can. J. Zool.* 64: 948-955.
- RUSSELL, A.P. AND BAUER, A.M. 1989. The morphology of the digits of the golden gecko, *Calodactylodes aureus* (Reptilia: Gekkonidae) and its implications for the occupation of rupicolous habitats. *Amph.-Rept.* 10: 125-140.
- SCHLEICH, H.H. AND KÄSTLE, W. 1986. Ultrastrukturen an Gecko- Zehen (Reptilia: Sauria: Gekkonidae). *Amph.-Rept.* 7: 141-166.
- UNDERWOOD, G. 1954. On the classification and evolution of geckos. *Proc. Zool. Soc. Lond.* 124: 469-492.
- ZWEERS, G.A. 1979. Explanation of structure by optimization and systemization. *Neth. J. Zool.* 29: 418-440.